Abiotic factors and biotic interactions jointly drive spider assemblages in nest-boxes in mixed forests

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Abstract. Although spiders are common inhabitants of tree cavities, factors that drive their community structure in these microhabitats are little known. Here we investigated whether bark type, season, intraguild predation (IGP) among spiders, and presence of vertebrate predators can influence the spider community structure in tree cavities. We examined spider abundance and the taxonomic and functional composition of spiders in nest-boxes within two mixed forest stands in central Slovakia in 2012–2013. In total, 1211 spiders belonging to 31 species were sampled from 60 nest-boxes at two sites over three seasons. Spider abundance peaked in autumn as spiders sought wintering sites. Guilds and taxonomic composition changed seasonally with spring and autumn communities dominated by "Other hunters" (Anyphaenidae, Clubionidae, Philodromidae) while during summer the community was dominated by "Sheet web weavers" (Linyphiidae). The guild and taxonomic turnover may be partly explained by the interaction between spiders' phenology and IGP exerted by winter-active spiders on smaller spiders from autumn until spring. Bark type influenced the guild composition as dominance of "Space web weavers" was higher in trees with rough bark than in trees with smooth bark. The rough bark also reduced the intensity of IGP by *Anyphaena accentuata* (Sundevall, 1833) on philodromids. The presence of insectivorous birds reduced the abundance of spiders by 67%. The presence of bird predators altered the guild composition as they affected mostly the web spiders. The results show that the biotic interactions and abiotic factors interactively determined the spider community structure in the nest-boxes depending on spiders' functional traits.

Keywords: Guilds, intraguild predation, predation, spiders, birds, cavities

Tree cavities are crucial microhabitats for a wide variety of animals in temperate and boreal forests. Cavities play an important role as a keystone vegetation structure and component in biodiversity conservation (Tews et al. 2004; Regnery et al. 2013). Cavities provide breeding, feeding and roosting habitat for hole-nesting birds (Bai & Mühlenberg 2008; Mainwaring 2011; Robles et al. 2011), small mammals (Czeszczewik et al. 2008; Regnery et al. 2013), social hymenopterans (Morato & Martins 2006; Broughton et al. 2015), earwigs (Burnip at al. 2002) and saproxylic beetles (Buse et al. 2007; Jansson et al. 2009; Sverdrup-Thygeson et al. 2010; Sebek et al. 2013).

The density of cavities depends on tree species composition in an area and increases with the age of forest stands (Larrieu & Cabanettes 2012). However, most cavity users (except certain primary cavity nesting birds) are not able to build their own cavities, and are, therefore, strongly limited by the availability of existing holes. In primeval forests, this limitation is reduced by a surplus of tree-holes with high structural variability (Wesołowski 2007) because of an absence of management practices. Most European forests have changed from old mixed forests to young monocultures of single-aged plantations due to human management (Bradshaw 2004; Gamfeldt et al. 2013) and nest-boxes are often used to enhance bird and small mammal breeding possibilities and abundance (Twedt & Henne-Kerr 2001; Czeszczewik et al. 2008). Furthermore, nest-boxes are frequently used as a method to study the life histories of inhabitants of natural cavities because natural tree cavities can be difficult to examine. Few studies have evaluated the benefits of bird nest-boxes for invertebrates (e.g., hymenopterans; Stanback et al. 2009; Langowska et al. 2010).

Spiders are the most dominant of invertebrate predators occurring on and under bark, in bark crevices as well as in tree cavities, and they play an important role in food webs of forests (Růžička et al. 1991; Lawrence & Wise 2004; Szinetár & Horváth 2006). Spiders depend on vegetation structures because they use tree microhabitats for hunting prey, feeding, roosting, overwintering, mating, etc. (Wunderlich 1982; Boyed & Reeves 2003; Horváth et al. 2005).

However, current knowledge about ecological factors which can influence the community structure of spiders in tree cavities is limited to few studies of nest-boxes (Conner et al. 1995; Naeem et al. 2010). For example, McComb & Noble (1982) found that spider assemblages in nest-boxes varied seasonally, and Naeem et al. (2010) tested effect of habitat and composition of nest contents on spider abundance.

Spider assemblages are controlled by environmental factors (e.g., humidity, temperature, habitat structure) and by biotic interactions (e.g., competition, intraguild predation, predation) (Wise 1993; Samu et al. 1999; Gunnarson 2007; Gan et al. 2015; Mammola et al. 2016; Petcharad et al. 2016). In forests, spiders are influenced by the structure of ground vegetation and tree crown canopies. It has been shown that structural components in different forests types composed of different tree species support different spider assemblages (Gunnarsson 1990; Pinzón & Spence 2010; Korenko et al. 2011; Samu et al. 2014; Košulič et al. 2016; Petcharad et al. 2016). Bark type and structure can also affect spider species richness as was demonstrated by Nicolai (1986) who found fewer species on smooth bark than on fissured, scaly bark in temperate forests.

Temporal scale patterns also have a strong impact on spider assemblages. In the temperate zone of Central Europe, there are significant seasonal variations in temperature. The

colonisation and re-colonisation of tree trunks after winter onset can be described as a seasonal dynamic for arboreal spiders (Hsieh & Linsenmair 2012). For example, the abundance of spiders in artificial shelters in apple trees is higher in autumn and winter and lower in spring and summer (Isaia et al. 2010).

Spider assemblages in tree cavities can be affected also by predation. Birds frequently use tree cavities for breeding and roosting and several foliage gleaning and bark foraging species are important predators of spiders (Gajdoš & Krištín 1997; Naef-Daenzer et al. 2000). Birds can effectively reduce spider abundance and diversity (Askenmo et al. 1977; Gunnarsson 2007; Mestre et al. 2013; Gunnarsson & Wiklander 2015). Birds are visually oriented predators; spiders make use of passive defenses to limit their detection and predation by birds (Pekár 2014). Bird predation can also influence the composition of spider guilds. Gunnarson and Wiklander (2015) found that actively hunting spiders are more prone to bird predation than web weavers while Mestre et al. (2013) found an opposite pattern. Hence, birds are not only able to influence the abundance and diversity of spiders, but they may also represent a selective pressure which structures the species composition of spider assemblages based on spiders' primary defense mechanisms and guild affinition.

Another biotic interaction that strongly shapes spider communities is intraguild predation among spiders (IGP) (Wise 1993). Although araneophagy is pronounced mainly in the hunting spiders (Michalko & Pekár 2016), they prey not only on other hunting spiders but also on web spiders such as theridiids and linyphiids (Gunnarsson 1985; Finke & Denno 2006; Korenko & Pekár 2010; Michalko & Pekár 2015). The top predator among spiders therefore will be a hunting spider but the impact of IGP might be mainly size-dependent in the tree cavities (Gunnarsson 1985; Korenko & Pekár 2010; Michalko & Pekár 2015).

In this study, we investigated how season, bark type (rough vs. smooth), presence of birds, and IGP among spiders influence the abundance, taxonomic and guild composition of spider assemblages in artificial tree-cavities. We conducted an exclosure experiment with guarded nest-boxes to test if the presence of vertebrate predators can negatively influence spiders inhabiting tree cavities. We analysed spider guilds and primary defences in relation to the presence or absence of birds using nest-boxes.

METHODS

Study area and sampling.—The study was performed in two managed forest habitats 7.5 km apart in the southeastern part of the Kremnické vrchy Mountains in central Slovakia. The first site represented a mature mixed 90-year old oak-hornbeam forest (Stráže, 48° 34′ 41″ N, 19° 5′ 35″ E, 320–380 m asl., hornbeam 48%, oak 46%). The density of natural tree hollows at this site was 28.7/ha and density of bird boxes was 1.4/ha. The second site is a 113 year-old beech-fir forest stand (Kováčová, 48° 38′ 12″ N, 19° 4′ 59″ E, 480–530 m asl., fir 42%, beech 40%); both areas have been a part of long term studies of bird roosting and foraging behavior (Krištín 2002; Veľký et al. 2010). The density of natural tree hollows on the plot is 22.9/ha and bird box density 1.3/ha.

These study sites are in a moderately warm region with a mean annual temperature of about 6.8° C (Barna & Schieber 2011). Both study plots are under active forest management. In each plot, we placed 30 wood nest-boxes (270 × 125 × 125 mm, inlet 33 mm) on trees two meters above the ground with southern orientation in 2011. Boxes were arranged 50–70 m apart in a straight line. All nest-boxes were checked during April, June and October in 2012.

To investigate the influence of spider predators (birds and dormice) on spiders, we conducted an exclosure experiment. In March 2013, for half of the nest-boxes ($n = 15$ per forest stand) we fenced entrances to prevent access of vertebrate predators. Nest-boxes were then treated as follows: the first nest-box was open while the following 2 nest-boxes were closed, 4 open, 3 closed, 3 open, 3 closed, 3 open, 3 closed, 4 open, 4 closed. Nest-boxes were checked twice (May 9, 2013 and July 3, 2013).

Data collection.—Spiders were collected from nest-boxes with an exhaustor (aspirator), by beating the roofs of nest-boxes outside the nest-box on a white sheet (while the box was covered by a reserve roof in order to minimize disturbance of breeding birds) and then by manually collecting from crevices in the interior. Spiders were then preserved in 95% alcohol for later identification. All specimens were identified to species whenever possible following Roberts (1996) and Heimer & Nentwig (1991) using the nomenclature in the World Spider Catalog (2016) Version 17.0. Voucher specimens were deposited in the Arachnid collection at the Institute of Forest Ecology SAS in Zvolen, Slovakia.

Season and bark type.—The analyses were performed with R (R Development Core Team, 2015) and Canoco for Windows 5 (ter Braak & Šmilauer 2012). We evaluated bark type visually according to bark structure and tree species as follows: "rough bark" being oak (*Quercus robur*) and fir (*Abies alba*); and "smooth bark" being beech (*Fagus sylvatica*), linden (*Tilia* sp.) and hornbeam (*Carpinus betulus*). There were 10 trees with rough bark and 20 with smooth bark in the first study site and 16 trees with rough bark and 14 with smooth bark in the second study site. We analysed the effect of bark type (i.e., rough, smooth) and season (i.e., spring, summer, autumn) on the abundances of spiders using Linear Mixed Effects Models (LME) and using the R package "nlme" as the data were potentially autocorrelated at several levels (Pinheiro et al. 2015). The first source of autocorrelation may occur from measurements performed in the two localities. The second source of autocorrelation could be tree species since unmeasured species-specific traits besides bark roughness can influence the abundances of spiders. We did not treat tree species as a fixed effect because we were unable to separate the confounding effect of locality as different tree species were sampled at the two localities. The third possible source of autocorrelation was the repeated measurements performed on individual trees. Values for spider abundances were log (x+1) transformed to approach normal distribution of errors (Pekár & Brabec 2012). The fixed effects of LME were represented by bark type and season, and their interaction. Locality, tree species and identity of tree represented the nested random effects in the initial model. We determined the structure of random effects by removing the random effects and comparing competing models with AIC (Pekár & Brabec 2012). Tree species with six levels was then the only random effect in the

final model. We did not consider species richness of spiders because abundances and species richness were highly redundant.

We investigated the effects of bark type and season on community composition at the family level. We studied how bark type and season influenced the taxonomic compositions of the spider community by Canonical Correspondence Analysis (CCA). We used CCA as the preliminary Detrended Canonical Analysis (DCA) indicated a unimodal response by the length of the first axis being 4.6 (Šmilauer & Lepš 2014). Families with fewer than three individuals were excluded from the analysis as CCA is sensitive to the presence of rare species (Šmilauer & Lepš 2014). First, we performed a global test of significance for explanatory variables (i.e., season, bark type) to avoid Type I errors resulting from multiple comparisons (Šmilauer & Lepš 2014). We then performed forward selection to investigate the significance of particular variables. Significance was tested by Monte Carlo permutation tests restricted within the localities (Šmilauer & Lepš 2014).

To investigate the effect of bark type and season on the guild composition of the spider community, we used the categories proposed by Cardoso et al. (2011) as they are connected to the trophic niches of spiders (Michalko & Pekár 2016) and so they can be considered as guilds (Root 1967). The guilds are: Other hunters, Ground hunters, Ambushers, Orb web weavers, Space web weavers, Sheet web weavers, Sensing web weavers, and Specialists (Cardoso et al. 2011). We employed univariate methods as we investigated the effect of only one functional trait, i.e., guild (Šmilauer & Lepš 2014). For each nest-box with at least one spider, we computed proportions of each guild. For statistical evaluation we used Generalized Estimating Equations (GEE) as an extension of Generalized Linear Models (GLM) for autocorrelated data (Pekár & Brabec 2012) using the R package "geepack" (Højsgaard et al. 2006). As the response variable was proportion, we used GEE with binomial error structure and logit link (GEE-b). The explanatory variables were guild, season, bark type and two-fold interactions of guild with season and of guild with bark type. Therefore, the linear predictor was of multifactorial ANOVA type. Here, we used the tree ID as the grouping variable. We opted for "exchangeable" correlation structure as the number of measurements per group were low (≤3; Pekár & Brabec 2012).

Predator effect.—Birds, as important predators of spiders, were the most abundant predators (98%) in the nest-boxes. However, rodents that constituted the rest of the potential predators (2%) can also prey on arthropods including spiders (Butet & Delettre 2011). To study the influence of predator presence on the abundance of spiders, we pooled all vertebrate predator species, which could be affected by our exclosure experiments (i.e., birds: *Ficedula albicollis* Temminck, 1815, *Parus major* Linnaeus, 1758, *Cyanistes caeruleus* Linnaeus, 1758, *Sitta europaea* Linnaeus, 1758; dormice: *Muscardinus avellanarius* Linnaeus, 1758, and *Glis glis* Linnaeus, 1766). These four bird species bred in all unfenced nest-boxes in both study sites during the exclosure experiment in following numbers: *F. albicollis* in 60% of nest-boxes (18/30), *P. major* in 26.7% (8/30) and *C. caeruleus* and *S. europaea*, in 6.7% each (2/30) and two dormice species we found each only in one nest-box check before the start of birds' breeding. So, we

compared the abundance of spiders between unprotected and protected (fenced) nest-boxes by LME as the data were autocorrelated. Data were log (x+1) transformed to approach normal distribution of errors (Pekár & Brabec 2012). The presence of predators acted as a fixed variable while locality and tree ID acted as nested random variables.

To compare the community composition with respect to the taxonomy, partial CCA with season and locality as covariates was used, as the initial DCA showed long environmental gradient (SD = 5.7). To compare the guild composition of spiders in nest-boxes that were protected and unprotected from predators, we used the classifications proposed by Cardoso et al. (2011) but we combined "Ground" and "Other hunters" and "Specialists" into "Hunters" because the way of movement and/or morphology of spiders should be more important for birds than their trophic niche. We also investigated the differences in composition of primary defense mechanisms of spiders. We classified primary defense mechanisms of each species according to data reviewed by Pekár (2014), i.e., anachoresis, crypsis, masquerade, aposematism and Batesian mimicry. The primary defense mechanisms of those species that were not included in the review of Pekár (2014) were derived according to the prevalence of defense mechanism found among their congeners. Any species which could not be categorized were omitted from analysis (n = 5). To investigate the effect of predator presence on the functional composition of spider communities, we computed the proportion of each guild / defense mechanism per nest-box. We compared the proportions of guilds and primary defenses between nest-boxes protected from predators and those unprotected using Generalized Mixed Effect Models with binomial error structure and logit link (GLMM-b) within the R package "glmmADMB" (Skaug et al. 2014). The guilds / defense mechanism, predator presence and their interaction acted as fixed variables and the linear predictor was of multifactorial ANOVA type. Tree ID acted as the random variable in the final model (Zuur et al. 2009). There was no need for correction of overdispersion.

Intraguild predation.—To investigate the possible effect of IGP on the spider community structure we used only the data for *Anyphaena accentuata* (Sundevall, 1833), *Philodromus* Walckenaer, 1826 spp., and Theridiidae in autumn as only these reached sufficient abundances for a reasonable statistical inference. In addition, IGP is well documented among these spiders (Michalko & Pekár 2015; Petráková et al. 2016). *Anyphaena accentuata* acts as a top predator in this system in autumn and can affect philodromids and theridiids (Pekár et al. 2015). During autumn, philodromids are larger than theridiids, which represent a substantial part of their diet (Gunnarsson 1985; Michalko & Pekár 2015). Therefore, we explored the effect of *A. accentuata* on theridiids and philodromids and the effect of philodromids on theridiids. Although clubionids also reached sufficient abundances, we did not include them as the biologically uninterpretable patterns or large misfits occurred in the models. We used GEE with Poisson error structure (GEE-p) as the response variable was counts and the data were autocorrelated (Pekár & Brabec 2012). Tree species represented the block variable and we used "exchangeable" correlation structure. The linear predictor was of ANCOVA type. The bark type acted as a
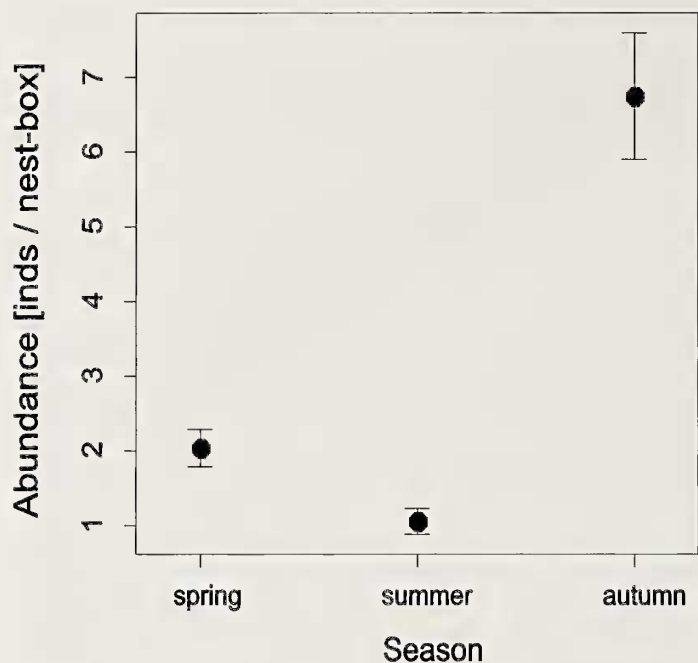
Figure 1.—Comparison of spider abundance in nest-boxes by vegetation season. Points and line segments show medians and SE, respectively; inds = individuals.

Figure 2.—CCA ordination diagram of spider families in relation to season.

factor whilst the abundance of the larger spider species acted as a covariate. We included also a quadratic form of the covariate because a hump-shaped relationship can arise. For example, both predators can respond positively at first (e.g., to prey availability or suitable environmental conditions), but as the interference intensifies the top predator starts to exclude the mesopredator (Holt & Polis 1997; Amarasekare 2008; Schmidt & Rypstra 2010; Schmidt et al. 2014). As the bark type can alter the intensity of IGP at the tree level, which can consequently translate in community composition in nest-boxes (Samu et al. 1999; Korenko & Pekár 2010), we included the interactions between bark and linear as well as quadratic form of the covariate. We employed Bonferroni adjustment of P-values to account for the multiple comparisons.

RESULTS

Spiders and birds were the most frequent inhabitants of the nest-boxes. Moths, earwigs, hymenopterans and small mammals were present in lower numbers, mostly outside the birds breeding season. In five nest-boxes, we found *Vespa crabro* nests (Hymenoptera). At both study sites, there were earwigs, *Chelidurella acanthopygia* (Géné, 1832) (Dermaptera) ($n = 73$), and *Lymantria* sp. (Lepidoptera) ($n = 112$). Two dormice species were found there: *Glis glis* ($n = 11$) and *Muscardinus avellanarius* ($n = 4$). Altogether five bird species were breeding and roosting in nest-boxes during both years; the most frequent and abundant bird species was *P. major* (41.9%, $n = 86$ occupied nest-boxes), followed by *F. albicollis* (37.2%), *S. europaea* (11.6%), and *C. caeruleus* and *Parus ater* (4.7% each). Altogether 633 spiders of 31 species from 13 families (from 1211 total specimens) were identified to species level (Appendix 1). Eight of these 31 species are exclusive bark-dwellers (i.e., habitat specialists), 16 are facultative bark dwellers and
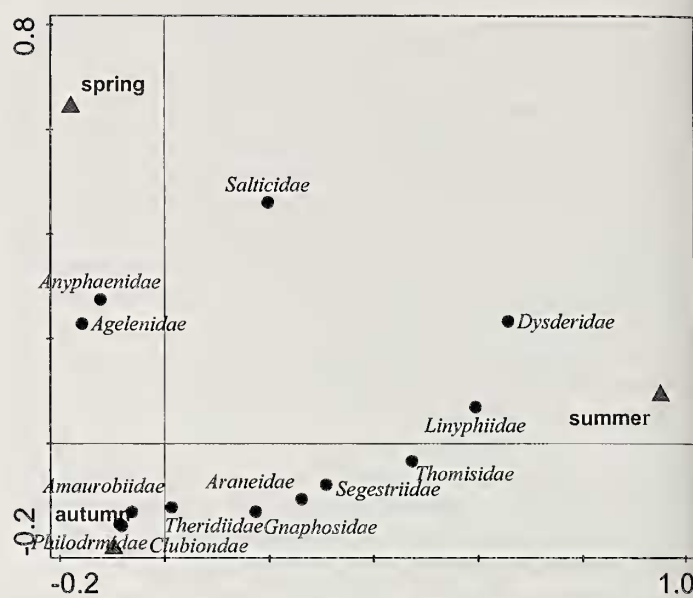
seven occur on the bark only accidentally (i.e., habitat generalists).

The two most abundant species were the arboreal and facultative bark dwelling *Anyphaena accentuata* which comprised 25% of all individuals, and the *Clubiona* Latreille, 1804 species complex (30%). Less abundant among our samples were *Platnickina tincta* (Walckenaer, 1802) with 9% and the *Philodromus aureolus* group (8%). The species *Arboricaria subopaca* Westring, 1861, also present in our samples, is listed as Vulnerable in the Red List of spiders of Slovakia (Gajdoš & Svatoň 2001).

Season and bark type.—The abundances of spiders significantly differed among seasons (LME, $F_{2,159} = 65.2$, $P < 0.001$, Fig. 1). Greatest abundances were in autumn (treatment contrasts, $P < 0.001$), followed by spring (treatment contrasts, $P < 0.002$), and summer. Bark type revealed no influence on overall spider abundances (LME, $F_{1,4} < 0.1$, $P = 0.97$).

Also community composition at the family level differed significantly only among seasons (CCA, pseudo-F $= 12.3$, $P = 0.001$; $R^2_{adj} = 0.14$, Fig. 2) and not between bark type (CCA, pseudo-F $= 0.8$, $P = 0.570$).

Season (GEE-b, $\chi^2_7 = 2120.8$, $P < 0.001$, Fig. 3A) as well as bark type (GEE-b, $\chi^2_{14} = 7348.4$, $P < 0.001$, Fig. 3B) influenced the functional community composition. In spring, the dominant guild was Other hunters, in summer Sheet web weavers, and in autumn Other hunters. The dominant guild on both bark types were Other hunters. The differences between the bark types was in the less dominant guilds, mainly Space web weavers (Fig. 3B).

Effects of predators.—The presence of predators significantly lowered the abundance of spiders in nest-boxes by 67% (LME, $F_{1,57} = 16.7$, $P < 0.001$, Fig. 4). There was no significant effect of the presence of predators on community composition of spiders at the family level (CCA, pseudo-F $= 1.0$, $P = 0.41$). However, the presence of predators influenced the functional composition of spider communities (GLMM-b, $\chi^2_4 = 10.6$, $P = 0.031$, Fig. 5). When predators were absent, the community was
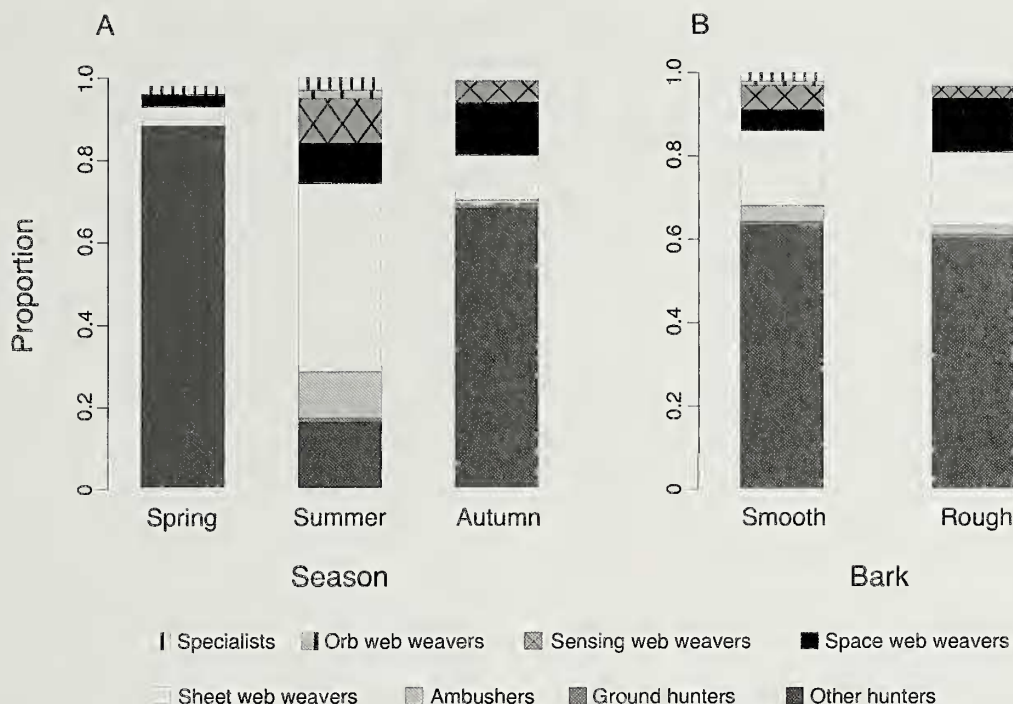
Figure 3.—Guild composition of spider communities in nest-boxes in relation to season (A) and bark type (B).

dominated by Sheet web weavers. When predators were present, the spider community was dominated by Hunters. However, there was no significant effect of predator presence on the composition of primary defense mechanisms in spider communities (GLMM-b, $\chi^2_2 = 0.3$, $P = 0.86$).

Intraguild predation.—There was a hump-shaped relationship between philodromids and *A. accentuata* (GEE-p, quadratic term, $\chi^2_1 = 9.3$, $P_{Bonferroni} = 0.006$, Fig. 6). The relationship differed between the bark types (GEE-p, interaction bark type: *Anyphaena*, $\chi^2_1 = 11.1$, $P_{Bonferroni} = 0.003$, Fig. 6). Consequently, in the smooth bark, the hump was not distinct as in the rough bark (Fig. 6). There was no significant
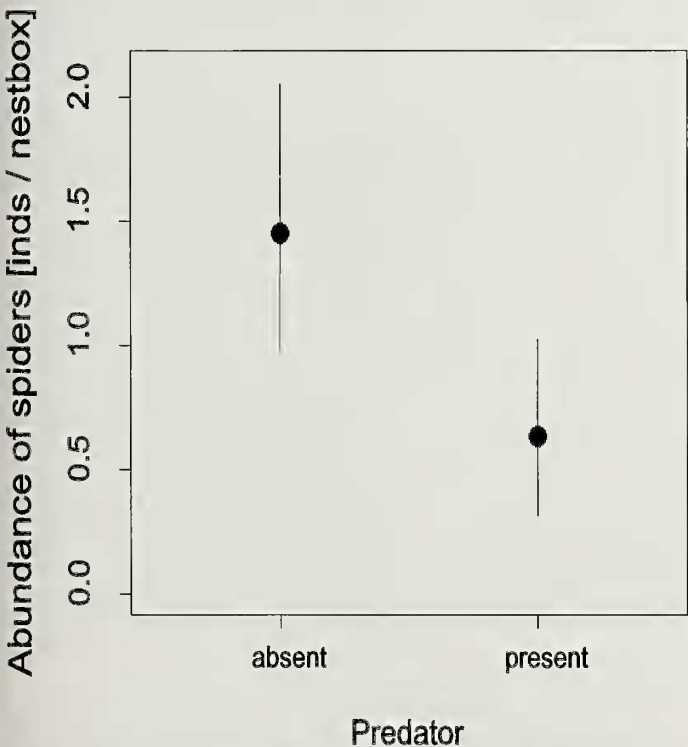

Figure 4.—Comparison of spider abundance in protected and unprotected nest-boxes. Points are medians and lines 95% CI; inds = individuals.
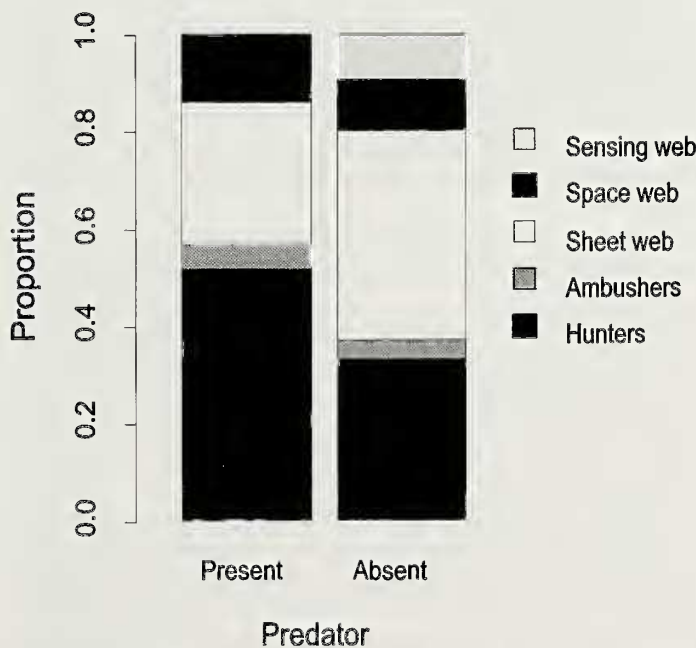

Figure 5.—Comparison of guild compositions of spider communities in protected and unprotected nest-boxes.
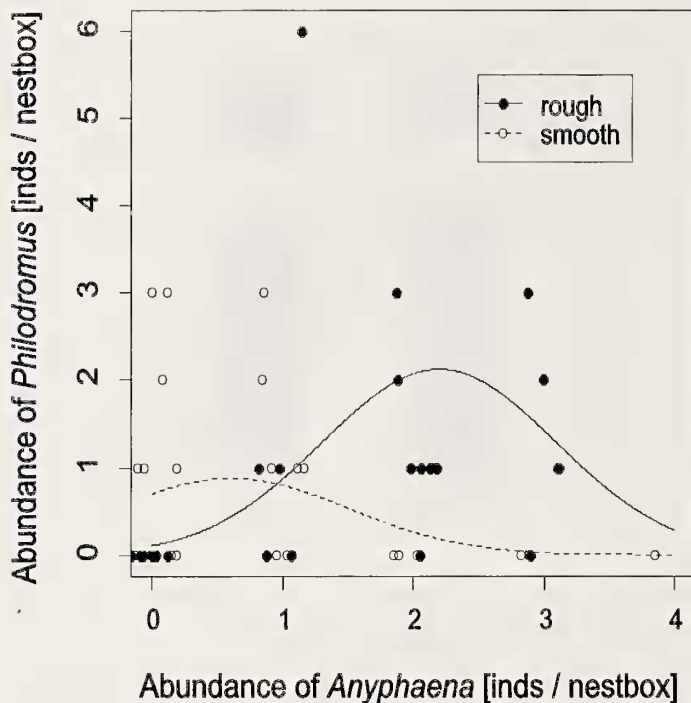
Figure 6.—Relationship between *Anyphaena accentuata* and *Philodromus* spp. abundances in nest-boxes in trees with different bark type. Small noise along the x-axis was added to show the data structure; inds = individuals.

effect of philodromids (GEE-p, $\chi^2_1 = 0.3$, $P = 0.560$) or *Anyphaena* (GEE-p, $\chi^2_1 = 0.1$, $P = 0.740$) on theridiids.

DISCUSSION

We analyzed how season, bark type, presence of predators, and IGP among spiders influence the abundance and composition of spider assemblages in artificial tree cavities. Spiders were the most common macro-invertebrates occurring in nest-boxes as was also found by Conner et al. (1995). Spiders that occupied nest-boxes were primarily facultative bark dwellers but exclusive bark dwellers and species accidentally on bark were also present (Szinetár & Horváth 2006).

Conner et al. (1995) found only minimal use of nest-boxes by birds because their study area included four different mature forest types which were not intensively managed and which contained many dead trees and natural cavities. In contrast, all nest-boxes were used by birds for breeding in our intensive managed forest study area during both years of study; similar results have been found by other ecological studies in this area (e.g., Krištín & Žilinec 1997; Krištín et al. 2001).

Season and bark type.—Season significantly influenced abundance as well as composition of spider communities. The abundances of spiders in the nest-boxes peaked in autumn when spiders sought crevices for overwintering. Horváth at el. (2005) found that the abundance of spiders on pine, *Pinus nigra*, increased from summer to fall in urban sites, but decreased or stayed stable in forests. We also found both a clear taxonomic and functional turnover from season to

season in the spider communities. In spring, assemblages were dominated mainly by *Anyphaena accentuata* categorized as Other hunters. In summer, communities were dominated by Sheet web weavers from the family Linyphiidae and in autumn again by Other hunters but with spiders *Clubiona* spp., *A. accentuata*, and *Philodromus* spp. The community dynamic might be, at least partly, influenced by the interplay between phenology of spiders and IGP. The interior of the nest-boxes were relatively homogeneous as their sides were smooth. The nest-boxes were also relatively poor in alternative prey other than spiders. Thus, IGP among spiders could be intense (Finke & Denno 2006; Riekers et al. 2006). In our system, the Other hunters were larger than the Sheet web weavers during spring and autumn. In addition, *A. accentuata* and philodromids are winter-active and prey even at temperatures close to 0°C (Pekár et al. 2015; Petráková et al. 2016). The winter-active Other hunters can therefore substantially reduce the abundances of smaller spiders from autumn until spring (Gunnarsson 1985; Pekár 1999; Petráková et al. 2016). In addition, as *A. accentuata* was a top predator among spiders in our system, the predation on other spiders during winter can explain its dominance in the nest-boxes during spring. Indeed, *A. accentuata* excluded philodromids already in autumn if it reached high abundances. During summer, the IGP on the small linyphiids could be alleviated as the Other hunters were scarce and/or they were small.

Although we did not find a significant effect of bark type on abundances or taxonomic composition at the family level, we found increased dominance of Space web weavers in trees with rough bark in comparison to smooth bark. Small Space web weavers build their webs in bark crevices and therefore the attachment points and shelters provided by the rough bark may represent a limiting resource for them (Roberts 1996; Goméz et al. 2016). Their increased abundance in trees might then translate into higher abundances of Space web weavers within nest-boxes.

Predator effect.—While spiders also occupied nest-boxes that were used by birds breeding or roosting, the presence of avian predators decreased the abundance of spiders in nest-boxes by 67%. This decline in spider abundance can be explained by diets of the birds using these nest-boxes. Species *P. major* and *F. albicollis*—common occupiers of nest-boxes in our study—are among the most important predators of spiders (Gajdoš & Krištín 1997; Krištín 2002, Pagani-Núñez et al. 2011). Although the adult birds do not usually forage within nest-boxes, older nestlings sometimes do (Krištín, unpubl.). Birds also may prey in trees nearby active nest-boxes and spider assemblages in the nest-boxes likely represent a sub-set of nearby available species and individuals. Moreover, the effect of birds on spiders may include also non-consumptive factors such as their mere presence, movement within nest-boxes, and web destruction which may induce spider emigration (Chmiel et al. 2000; Werner & Peacor 2003; Goncalves-Souza et al. 2008; Mestre et al. 2014; Bucher et al. 2015).

We found no significant difference in the kinds of primary defense mechanisms of spiders in comparing protected and unprotected nest-boxes. The defense mechanisms of spiders observed in our study are most effective against visually oriented predators (Pekár 2014). The insides of nest-boxes are

very dark and certain defense mechanisms may not function well under such dark conditions. Alternatively, all mechanisms were equally effective against avian predators. Nevertheless, we found that the presence of predators affected the community composition with respect to spider guilds, which is known to influence the risk of being preyed upon by birds (Gunnarson 2007; Mestre et al. 2013; Gunnarson & Wiklander 2015). Gunnarson & Wiklander (2015) have found that Hunters are exposed to the higher predation risks than Web weavers. One explanation provided by those authors was that the webs can protect spiders from birds. In contrast, we found that the presence of birds reduced the proportions of Sheet web weavers and Sensing web weavers, while the proportion of Hunters increased. Similar pattern was observed by Mestre et al. (2013). The stronger effect on web weavers in our study can be due to destruction of webs by birds, which led to the spider emigration. The web weavers might also be outside their webs where they are clumsier than hunters and are, therefore, more prone to bird predation.

Intraguild predation.—We found a significant relationship between *A. accentuata* and philodromids, which was influenced by the bark type. The influence of bark type on this relationship indicates that the processes at the tree scale influenced the community composition at the nest-box scale. In the rough bark, there was a hump-shaped relationship between abundances of philodromids and *A. accentuata*. This means that both species positively responded to some factors at first (e.g., prey availability, suitable microhabitat conditions, vertebrate predator free space), but as the interference intensified *A. accentuata* excluded the philodromids. In the smooth bark, the abundances of philodromids basically only declined with increasing abundance of *A. accentuata*. The rough bark reduced the intensity of IGP because it can provide small crevices that are not accessible for large *A. accentuata* and so they can serve as the enemy-free shelters for the smaller philodromids (Korenko & Pekár 2010). The exclusion of philodromids could be due to consumptive effect as predation evinced by *Anyphaena* on philodromids can be severe (Korenko & Pekár 2010; Petráková et al. 2016). The exclusion can be also due emigration caused by trait-mediated effect or direct non-consumptive interference (Sehmidt & Rypstra 2010; Mestre et al. 2014; Schmidt et al. 2014).

In conclusion, our study provides a better understanding of the processes affecting the distribution of spider assemblages in tree cavities. The community of spiders in nest-boxes was affected by season, bark type, predation by birds, IGP among spiders and interaction among the abiotic and biotic factors depending on spider functional traits, namely guild association and size. Our results from the exclosure experiment support strong negative effects of birds especially on web-building spiders. Finally, our study suggests that use of nest-boxes is an effective method for evaluation of arboreal spider assemblages. Nest-boxes provide refuge for spiders and serve as useful alternatives to tree hollows and tree bark.

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Appendix 1.—Spider guilds, defense mechanism and number of individuals sampled in nestboxes during all seasons with emphasis on bark type in 2012, and in protected (fenced) and unprotected nest-boxes during exclosure experiment in 2013 in two mixed forests.

Family / Species	Season			Bark type		Experiment		Guilds	Defense mechanism
	Spring	Summer	Autumn	Rough	Smooth	Unprotected	Protected		
Dysderidae									
Harpactea hombergi (Scopoli, 1763)	0	0	0	0	0	7	11	specialist	batesian mimicry
Segestridae									
Segestria senoculata (Linnaeus, 1758)	0	7	9	3	13	3	3	sensing web	crypsis
Theridiidae									
Cryptachaea riparia (Blackwall, 1834)	0	1	0	0	1	0	0	space web	anachoresis
Platnickina tincta (Walckenaer, 1802)	2	1	43	23	23	0	3	space web	
Steatoda bipunctata (Linnaeus, 1758)	0	0	0	0	0	1	0	space web	anachoresis
Theridion mystaceum L. Koch, 1870	0	0	0	0	0	3	3	space web	crypsis
Theridion varians Hahn, 1833	0	1	0	1	0	0	0	space web	crypsis
Theridion spp.	1	3	10	10	4	5	5	space web	crypsis
Linyphiidae									
Drapetisca socialis (Sundevall, 1833)	0	5	0	4	1	1	2	sheet web	crypsis
Leptyphantes leprosus (Ohlert, 1865)	0	1	6	0	7	2	3	sheet web	anachoresis
Moebelia penicillata (Westring, 1851)	0	2	0	2	0	0	0	sheet web	not available
Leptyphantes spp.	4	16	5	13	12	5	4	sheet web	anachoresis
Araneidae									
Araneus diadematus Clerck, 1757	0	0	2	0	2	0	0	orb web	crypsis
Nuctenea umbratica (Clerck, 1757)	0	1	0	1	0	0	1	orb web	anachoresis
Agelenidae									
Agelena labyrinthica (Clerck, 1757)	0	0	1	0	1	0	0	sheet web	anachoresis
Tegenaria silvestris L. Koch, 1872	0	0	0	0	0	1	1	sheet web	crypsis
Tegenaria ferruginea (Panzer, 1804)	2	0	0	2	0	0	5	sheet web	crypsis
Amaurobiidae									
Amaurobius fenestralis (Ström, 1768)	2	2	15	7	12	4	14	sheet web	anachoresis
Anyphaenidae									
Anyphaena accentuata (Walckenaer, 1802)	91	3	69	87	76	10	5	other hunters	not available
Clubionidae									
Clubiona comta C.L.Koch, 1839	0	0	0	0	0	1	1	other hunters	anachoresis
Clubiona corticalis (Walckenaer, 1802)	0	0	2	0	2	1	1	other hunters	anachoresis
Clubiona marmorata L. Koch, 1866	0	0	1	1	0	1	0	other hunters	anachoresis
Clubiona pallidula (Clerck, 1757)	0	0	0	0	0	1	6	other hunters	anachoresis
Clubiona spp.	10	2	204	103	113	0	2	other hunters	
Gnaphosidae									
Arboricaria subopaca Westring, 1861	0	0	0	0	0	1	0	ground hunters	crypsis
Zelotes apricorum (L. Koch, 1876)	0	0	0	0	0	1	0	ground hunters	anachoresis
Haplodrassus sp.	0	0	0	0	0	1	0	ground hunters	not available
Scotophaeus sp.	0	1	3	2	2	2	2	ground hunters	anachoresis
Philodromidae									
Philodromus aureolus group	2	1	27	24	6	0	0	other hunters	crypsis
Philodromus margaritatus (Clerck, 1757)	0	0	18	4	14	0	0	other hunters	crypsis
Thomisidae									
Diaea dorsata (Fabricius, 1775)	0	0	2	2	0	0	0	ambush hunters	crypsis
Ozyptilla sp.	0	0	0	0	0	1	1	ambush hunters	not available
Xysticus sp.	0	5	1	2	4	2	2	ambush hunters	crypsis
Salticidae									
Ballus chalybeius (Walckenaer, 1802)	0	1	0	0	1	0	3	other hunters	batesian mimicry
Heliophanus dubius C. L. Koch, 1835	0	0	0	0	0	1	0	other hunters	batesian mimicry
Marpissa muscosa (Clerck, 1757)	2	0	0	1	1	1	1	other hunters	crypsis
Pseudeuophrys erratica (Walckenaer, 1826)	0	6	0	0	6	1	5	other hunters	not available
Salticus scenicus (Clerck, 1757)	0	0	0	0	0	1	0	other hunters	crypsis
Salticus zebraneus (C. L. Koch, 1837)	0	0	0	0	0	1	0	other hunters	crypsis
Total	116	59	418	292	301	44	92		